Taste discrimination in lemurs and other primates, and the relationships to distribution of plant allelochemichals in different habitats of Madagascar

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TASTE DISCRIMINATION IN LEMURS AND OTHER PRIMATES, AND THE RELATIONSHIPS TO DISTRIBUTION OF PLANT ALLELOCHEMICALS IN DIFFERENT HABITATS OF MADAGASCAR

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Abstract

This chapter deals with the adaptation of taste responses of lemurs and other primates to different environments, in relation to primary and secondary compounds in potential foodstuffs. Emphasis is placed on the relationship between taste sensibility to sugars and energy expenditure across species. In the most specialized species, the adaptive trends are inferred according to the importance of the deviation from such allometric relationship. The signification of sugar mimics present in some fruits is discussed in terms of coevolution of plants and tasting ability of primates, that, for lemurs, parallels that of platyrrhine monkeys.

Taste responses towards other tastants such as sodium chloride are examined in relation to potential risks of deficiency and/or toxicity. Sensitivity to tannins has been investigated in different species, with a two-bottle preference test. We observed large variations that are likely to be adaptive to the concentrations in plant species in various environments. For instance, the rejection threshold for a mixture of tannin and fructose is much higher in *Propithecus verreauxi* (above 170 g/l) than in *Microcebus murinus* (0.54 g/l). Recognition thresholds can also vary slightly between human populations, in relation to ancient or recent food practices. There is also a wide range of taste sensitivity towards quinine, without any correlation, in this case, with body mass or other factors related to energy expenditure.

Different habitats of Madagascar are compared according to the results of screening tests on tannins and alkaloids. The eastern rain forest (at Andasibe) present slightly lower proportion of plants with alkaloid-like reaction, and a significantly higher proportion of tannin-rich plants than both the gallery forest and the Didiereaceae bush in the south (at Berenty). The results have been related to the gustatory ability of lemur species having to cope with these secondary compounds, and the food niche of the different species.

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Résumé

Nous présentons, dans ce chapitre, les adaptations de la sensibilité gustative des lémuriens et des autres primates à différents environnements, en fonction de la teneur des aliments potentiels en composés primaires et secondaires. Nous montrons d'abord l'importance d'une relation d'allométrie entre la sensibilité aux sucres et les besoins énergétiques des différentes espèces. Les tendances vers un régime alimentaire spécialisé se traduisent par une déviation par rapport à la tendance moyenne rapportée au poids corporel de l'espèce. Nous montrons également des exemples de coévolution entre les possibilités de perception des produits sucrés par les primates et l'apparition de substances dont le goût mime celui des sucres dans différents environnements. Dans ce cas, il existe un parallélisme entre les possibilités de perception des primates platyrrhiniens et celle des lémuriens.

Les réponses vis-à-vis d'autres substances auxquelles réagissent les organes de la gustation, comme par exemple le chlorure de sodium, sont discutées en fonction des risques de carence ou des possibles effets toxiques. La sensibilité aux tannins a été étudiée chez différentes espèces, en fonction d'un test comportemental de préférence-évitement. De ce point de vue, il existe d'importantes différences entre primates, susceptibles de correspondre aux possibilités d'adaptation aux concentrations des tannins dans les espèces végétales des différents milieux. Par exemple, le seuil d'évitement d'un mélange de tannin et de fructose est beaucoup plus élevé chez le propithèque, *Propithecus verreauxi* (plus de 170 g/l) que chez le microcèbe, *Microcebus murinus* (0,54 g/l). Les seuils de reconnaissances des tannins peuvent également varier, mais dans une moindre mesure, chez les populations humaines, en relation avec une adaptation ancienne ou relativement récente des pratiques alimentaires. De la même façon, on observe des différences de sensibilité à la quinine ; mais dans ce cas il n'existe aucune relation avec la masse corporelle ou tout autre paramètre relatif à la dépense énergétique.

Nous avons comparé, dans différents habitats de Madagascar, les fréquences des tannins et des alcaloïdes, en fonction des résultats de tests préliminaires (*screening*). Dans la forêt dense humide de l'est (à Andasibé), nous avons trouvé une proportion sensiblement inférieure à celle des forêts du sud (forêt galerie et bush à Didiereaceae de Berenty) de plantes susceptibles de contenir des alcaloïdes. Au contraire, en ce qui concerne les teneurs en tannins, la proportion est nettement plus élevée dans la forêt humide de l'est que dans les deux autres environnements étudiés. Ces résultats ont été rapportés à ce que nous savons des adaptations gustatives et des comportements alimentaires des différentes espèces de lémuriens confrontées aux produits secondaires de ces habitats.

Introduction

Recent advances in the field of taste physiology have revealed that most of the taste bud sensory cells of the primate tongue respond to several substances, having higher affinities for some of them (Faurion, 1987). The shape of the signal elicited on gustatory nerves is the result of the combined firing of all these cells. It is a kind of "signature" differing more or less in the various tasting substances, an evidence that left to rest the old idea of the "four basic tastes" (Faurion, 1993 ; Hladik & Simmen, 1996).

There are, nevertheless, categories of substances (sugars, acids, etc.) that elicit taste signals with such resembling shapes that, for non human primates and humans, it is not easy to discriminate among different products within each category, even at high concentration. The occurrence of such

classes of tasty substances among natural products is related to the evolutionary trends in food nutrient content and toxicity, and linked to sensory perception of potential consumers.

As diets have evolved in past and present environments, tastes have responded adaptively, especially in order to maximize energy intake. In turn, food plants have evolved nutrients and toxins in relation to the tasting abilities of consumers. These compounds can be beneficent or harmful in various environments and at different concentrations, as shown by the examples discussed in this chapter.

Taste abilities of lemurs and other primates are presented in terms of thresholds and above-threshold responses to potential foods. The method of investigating taste ability in non-human primates is based on a standard behavioral testing procedure: the "two-bottle test" (Glaser, 1979 ; Simmen & Hladik, 1988). Consumptions of a tastant solution and tap water presented simultaneously are measured using various concentrations of the tastant, to determine the lowest concentration that is "discriminated". Although the behavioral thresholds of some primate species were quite similar to thresholds obtained by directly recording signals on a peripheral taste nerve (Glaser & Hellekant, 1977), the results must be carefully interpreted because the test provides information on both taste discrimination and preference.

Sugar discrimination

Lemurs, as most non-human primates, include fruits in their diet. The form and function of the digestive system (including taste perception) have been shaped in parallel to the evolution of fruit-bearing plants following the Mezozoic (Hladik & Chivers, 1994; Simmen, 1994). Although variable across plant species and in relation to ripening (Bollard, 1970), fruit composition generally includes soluble forms of sugars – mainly fructose, glucose and sucrose.

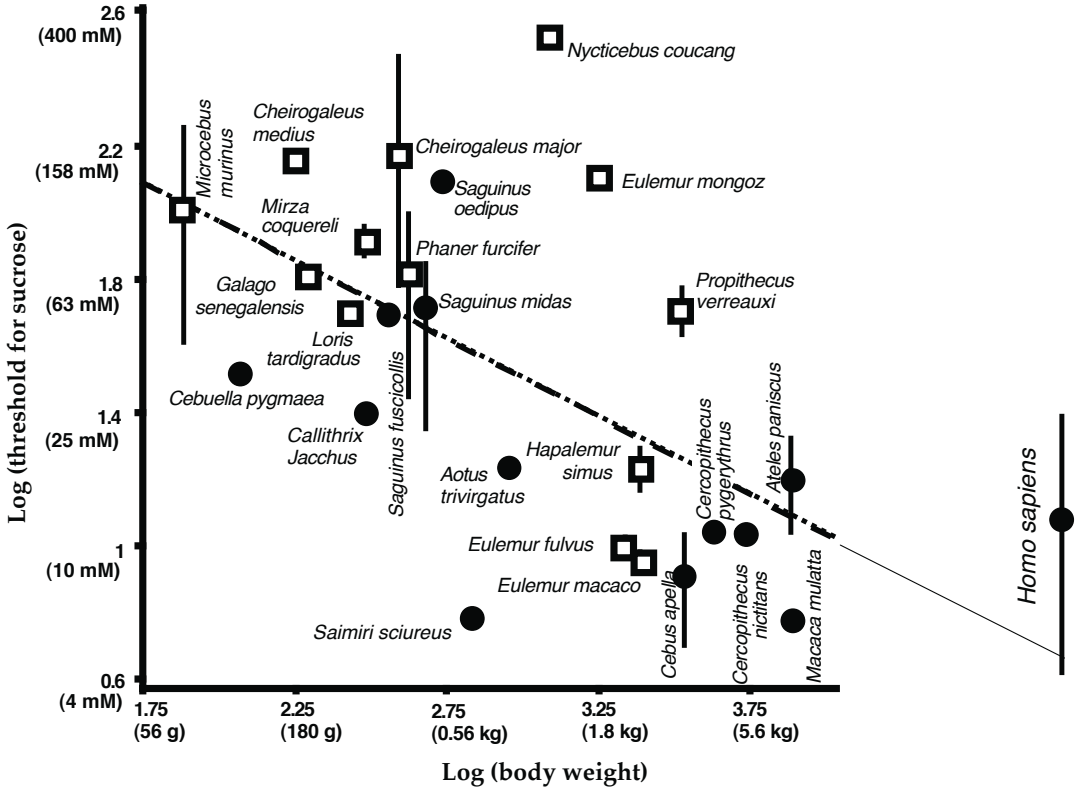

Figure 1. Allometric relationship between taste sensitivity to sucrose and body mass in lemurs (squares) and other primates (circles); data from Simmen and Hladik (1998); Hladik and Pasquet (in press).

The thresholds for sucrose, which are known for 33 non-human primate species (Simmen & Hladik, 1998), vary between 6 and 330 millimoles/l (that is 2 to 113 g/l). Since these "behavioral thresholds" are the minimum concentrations that remain attractive, most ripe fruits have a sugar content that can actually be tasted and produce a sensory reward in most primate species.

For lemurs, as for other primates, including humans (Fig. 1), the threshold for sucrose is correlated with species body mass, the larger the species, the better taste acuity (*i.e.* low threshold). There is a similar correlation between taste ability and body mass for fructose, although less data are available regarding thresholds (Simmen & Hladik, 1998).

These relationships may reflect the importance of taste acuity to improve foraging efficiency, since large body-sized primates perceive a wide range of sugar concentrations as palatable and can use a wide array of foodstuffs.

The adaptive trends are revealed by shifts from the regression line, although the wide scatter of data is partly due to inaccuracy or differences between the methods used to measure thresholds. Among primate species differing noticeably from the common pattern (*i.e*. located outside of the regression line), the slow loris, *Nycticebus coucang*, exhibits a high taste threshold, presumably corresponding to a generalized decrease in taste sensitivity. This allows the use of pungent insects and other prey unpalatable to most primates (Hladik, 1979). In contrast, the eclectic frugivorous diet of the squirrel monkey, *Saimiri sciureus*, would necessitate a taste acuity better than predicted by the allometric function to cope with the high energy expenditure of foraging in extremely large home ranges (Terborgh, 1983).

Furthermore, there is a dichotomy in taste ability for peculiar sweeteners (protein sugar mimics such as monellin and thaumatin) between New World and Old World primates, including humans, and lemurs appear, in this respect, as close to platyrrhines (Glaser et al., 1978). For instance, the fruit of a rain forest species of west Africa, *Thaumatococcus daniellii*, has a very sweet pulp around the seeds, but almost no sugar. The corresponding sweetener, thaumatin, is tasted by Old World primates, but not by lemurs and New World primates.

Species differences in the ability to discriminate the very strong sweet taste (as perceived by humans) of such natural sweeteners are most likely explained by different binding mechanisms on chemoreceptors. Protein evolution in taste receptors would have followed species diversification, after catarrhine and platyrrhine primates evolved separately on the Old World and American continental plates respectively. In their corresponding rain forest environments, flowering plants competing for seed dispersal evolved fruits containing large amounts of sugars; the more sugar, the more efficient their dispersal by consumers. As a result, genes coding for the fortuitous emergence of proteins with tastes mimicking those of sugars would have been selected for. Primates feeding on these fruits of the African rain forest are "tricked" by the plant species for which they work as seed dispersers without receiving any energy in return (although they obtain a sensory reward).

In Madagascar, from this viewpoint, prosimian taste perception remained closed to that of the present platyrrhine primates of the New World, and the plants bearing fruits with sugar mimics have not been observed in the various Malagasy habitats. Nevertheless, one can wonder whether homologous forms have evolved, that have not yet been detected, since sugar mimics tasted by prosimians would be tasteless for humans whose taste buds have typical characteristics of catarrhine primates.

Taste sampling of soluble sugars allows high energy intake through immediate preference; but this example cannot be generalized to other high-calory foodstuffs. Indeed, several nutritious foods have little taste, including most plant parts containing starch or fat (such as tubers, nuts, and grains), the staple foods of human populations. The apparently imperfect taste response to these highly nutritious compounds (as compared to clear-cut responses to soluble sugars) could be related to the relatively recent radiation of flowering plants. Whereas sugars – always present in plant metabolic pathways – may have been concentrated in fruits of the early angiosperms, fatty fruits seem to be the result of a more recent and sophisticated evolutionary process (McKey et al., 1993). In this case, the trend towards reduction in the size of the fruits is compensated by a high caloric density, and the reward (in terms of energy intake), although determined by a delayed response of the organism, can be associated to other cues of taste perception for an immediate sensory reward.

Discrimination of other tastants

The positive responses to sodium chloride of most mammal species have been considered as adaptive. However, mineral deficiencies are unlikely to occur among wild primates, especially in forest environments where available foods provide higher dietary supplies than estimated requirements (Hladik & Gueguen, 1974). Sodium chloride (which is harmful only if ingested in too large amounts) is present at low concentration in most plant parts (less than 0.5 % of the dry weight, that is below 20 mM concentration). The resulting salty taste is unperceivable for most primates, which have thresholds ranging between 5 mM and 500 mM. In this context of low risk of mineral deficiency, one may question whether geophagy plays a role in mineral nutrition.

Indeed, clay and other phyllitous soil materials eaten by primates can also work as adsorbent of tannins of the stomach content. This beneficent effect is the most likely explanation for geophagy during the periods of intense feeding on mature leaves that contain digestibility reducers such as tannins.

Tannins are widespread in plants (Bate-Smith, 1974), known for their role as a chemical defence preventing destruction by predators (Swain, 1979). The biological effect derives from: (1) a repellant taste, that renders the plant tissues unpalatable, (2) affinity to bind with proteins and to form insoluble complexes, reducing the digestibility of protein (see review in Haslam, 1989). Several primate species select plant parts with low levels of tannins (Ganzhorn, 1988) whereas other species appear to tolerate large amounts (Struhsaker et al., 1997).

Recently, a gallotannin has been shown to elicit a signal on a branch of the chorda tympani - the proper nerve which conveys only gustatory signals - of *Microcebus murinus* (Hellekant et al., 1993). The same tannin produces responses in the neurones of the orbitofrontal cortex (secondary taste area) of *Macaca fascicularis* (Critchley & Rolls, 1996). The results suggested that astringency corresponds to one or several taste qualities.

In terms of plant adaptive strategies, tannins are efficient only when large amounts are present to deter herbivores. Condensed tannins in fruits – and their distasteful taste – tend to decline during maturation, simultaneously with the increase of sugars; the taste response is necessarily directed towards the resulting mixtures. For instance, Simmen (1994) showed that *Callithrix jacchus* and *Callimico goeldii,* which have similar perception of fructose, tolerate tannin/fructose mixtures, but reject them when the tannic acid reaches 4% of the fructose content (that is 0.4 g/l for a moderately sweet solution). Nevertheless, the more sugar in the mixture, the more tannin tolerated.

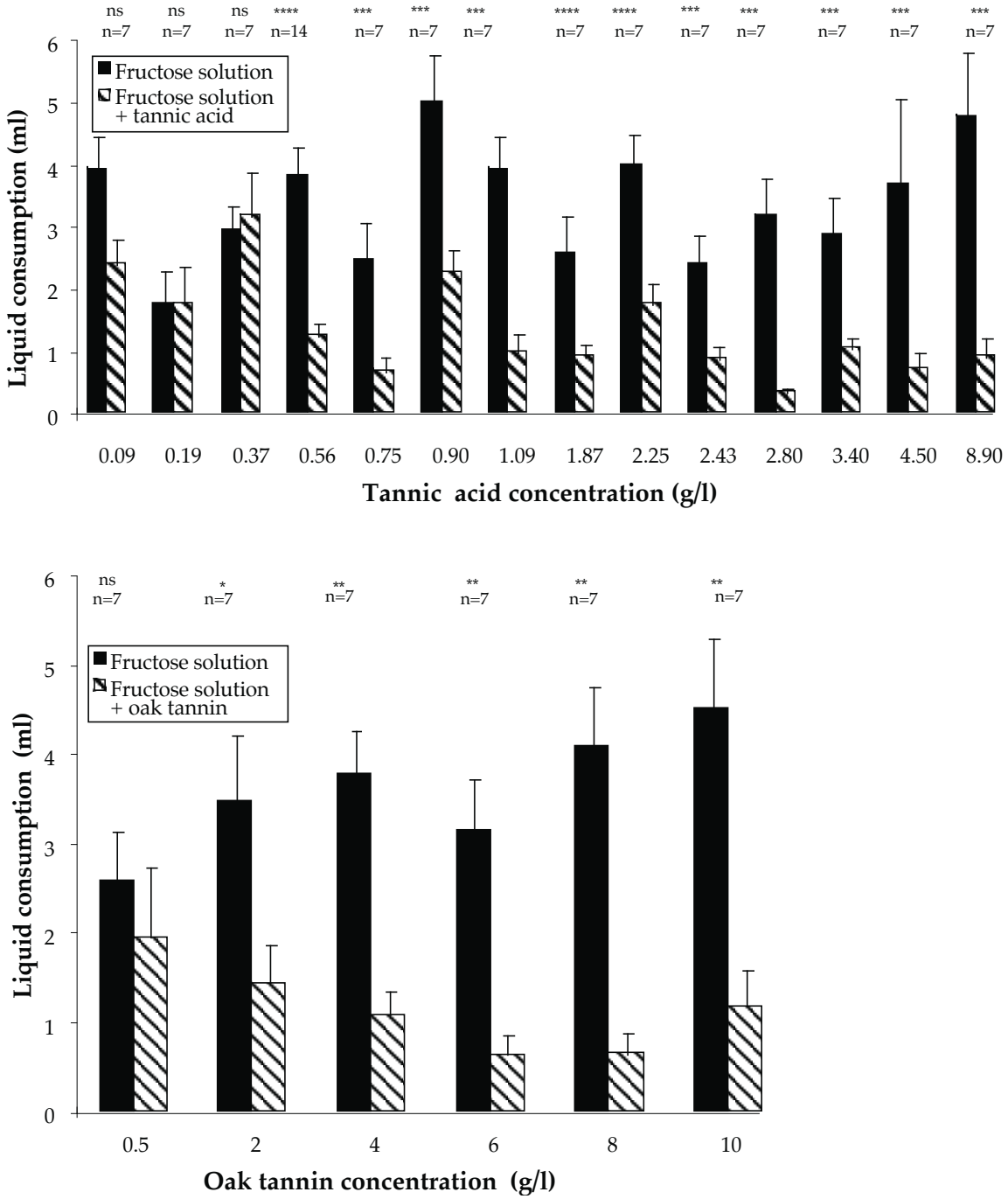

Figure 2. Ingestive responses of male *Microcebus murinus* towards binary solutions of fructose and tannin (upper: tanic acid; lower: oak tannin) versus pure fructose solution in a two-bottle test. The fructose concentration is held constant at 100 mM whereas tannin concentration is varied in each test. The inhibition threshold is defined as the lowest tannin concentration for which the mean difference of consumption between mixture and sweet solution is significant (paired-sample *t*-test).

In *Microcebus murinus*, the behavioral method, (Two-bottle test) was used to measure differences of consumption between a solution of fructose at 100 mM vs the same solution added with tannins (tannic acid, oak tannin). The inhibition threshold was defined as the lowest tannin concentration for which the mean difference of consumption between mixture and sweet solution is significant (paired-sample *t*-test). The inhibition threshold corresponds to 0.54 g/l for tannic acid and to 2.0 g/l for oak tannin, that is between 3 and 11% of the weight of fructose added to the solution (Fig. 2). This is a level corresponding to tannin concentration in many unripe fruits, a concentration that varies throughout the ripening process (Van Buren, 1970). For example, immature fruits eaten by chimpanzees, may contain 5 % (12 g/l assuming 80% moisture in fruits) of condensed tannins

(Wrangham & Waterman, 1983). As demonstrated by Simmen et al. (in press), the tolerance of tannins is dependant upon the concentration of sugar, which corroborates the idea of a trade-off between acceptable levels of tannin and nutrient content, mediated by oropharyngeal sensations. The electrophysiological recordings obtained from the chorda tympani of *Microcebus murinus* proper nerve showed that tannic acid elicits a reponse at 0.34 g/l and no response at 0.21 g/l (Hellekant et al., 1993). Since astringency of tannic acid may partly be masked by sweetness (Lyman & Green, 1990), the results, using either electrophysiological or behavioral methods, are concordant.

The recognition thresholds were also determined for humans, as part of a European Union program, with a blind test during which tannic acid, oak tannin, and various non-tannin substances, were presented at random, starting from the weakest concentrations (Iaconelli et al., 1998). The individual recognition threshold is the lowest concentration for which the taste can be described according to standard quality labels (sweet, sour, salty, bitter or astringent). The recognition thresholds for tannins varies among European populations between 0.32 and 0.79 g/l for oak tannin, and between 0.22 and 1.15 g/l for tannic acid. Significant differences ($p<0.05$) between the north samples (France) and the south samples (Italy + Spain) for both tannins have been found, the latter having higher thresholds. Alimentary inquiries indicate that the proportion of astringent products in the diet was much higher in mediterranean populations (astringent vegetables, olive oil, oak acorn, chestnut, red wine, lemon, and grape). Either dietary or genetic factors may influence the recognition threshold for astringent taste.

Taste and feeding selectivity in various environments

Taste thresholds for quinine vary widely – from 0.8 to 800 micromoles per liter (μM) – among non-human primates; but in contrast to what was observed for sugars, no relationship could be found between the taste sensitivity to quinine and the body mass of different species (Fig. 3). A wide range in sensitivity may reflect the adaptations of different primate species to different nutritional environments, as exemplified by the two marmosets, *Callithrix argentata*, living on white-sand riverine forests, and *Cebuella pygmaea*, inhabiting the interior of the rain forest. Both species feed mainly on the gum exuded by a tree bark after they have gouged it with their incisors. These primates are in contact with bark substances evolved by tree species as chemical defences (for instance quinine is a chemical substance in cinchona bark). However, due to the peculiar environment where these marmosets live in, the alkaloid content and toxicity of the bark is likely to vary. Contrary to rain forests, where there is little risk of eating bitter plants – because most alkaloids, such as caffein, are not likely to be highly toxic – forests with less diversified flora (such as that inhabited by *Callithrix argentata*) present a higher risk, that can be avoided by an extreme sensitivity to quinine.

In fact, plant parts are frequently selected for on the basis of low content of alkaloid and/or tannin. But this is not a general rule. In the Gabon rain forest, for example, where 14% of the plant specimens (among 382 species tested) react positively to the alkaloid test, the chimpanzee includes in its diet a similar proportion (15%) of plants likely to have a high alkaloid content. Accordingly, since chimps have no particular detoxification system, most alkaloids in this environment can be compared to caffein in their weak toxic effect (Hladik & Hladik, 1977). Furthermore, the observations of Huffman and Seifu (1989) of chimpanzees, in a montane forest, "curing themselves" with a bitter plant species, *Vernonia amygdalina*, usually discarded by healthy individuals, provide evidence that the aversive response to alkaloids can be reversed.

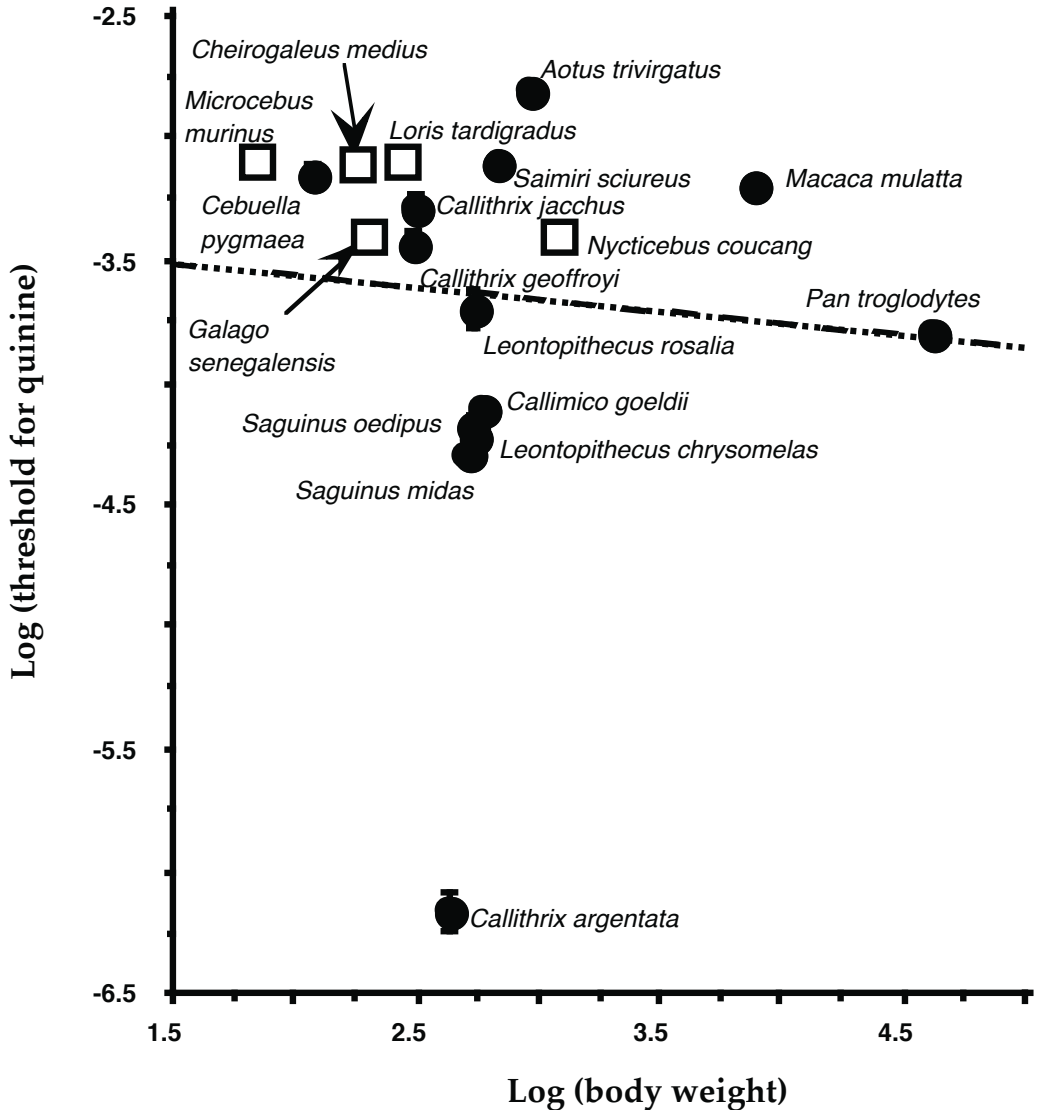

Figure 3. Relationship (without allometry) between taste sensitivity to quinine and body mass in lemurs (squares) and other primates (circles); data from Simmen and Hladik (1998).

Our recent observations in various environments of Madagascar, also provide evidence of the variation of tannin and alkaloid occurrence, with which lemurs have to cope, but the question of whether Malagasy prosimian species differ in their tolerance of plant secondary compounds has been little investigated so far. In the eastern rain forest of Andasibe, niche partitioning has been inferred on the basis of species ability to feed on plants containing alkaloids and tannins (Ganzhorn, 1988). In captivity, primate species exhibit distinct taste discriminative thresholds for quinine hydrochloride and tannic acid (see above).

Plants were collected in the eastern rain forest at Andasibe and in the gallery forest as well as in the spiny Didiereaceae bush in southern Madagascar (Berenty). The screening of alkaloids was performed using Mayer's and Dragendorff's reagents. For phenolic compounds, we used ferric chloride and salted gelatine. The occurrence of these secondary compounds is determined according to the precipitate obtained when adding the reagents to solubilized leaf samples. The amount of the precipitate is expressed on a scale ranging from 0 to +++ (Table 1; see detailed results in Appendix).

Table 1. Comparison of a mid-montane rain forest of the east of Madagascar (Andasibe) with two southern habitats, the gallery forest and the Didiereaceae Bush (at Berenty), according to the screening of phenolics and alkaloids in mature leaves. The significance of the differences derives from Chi-square tests (**: $p \leq 0.01$; ***: $p \leq 0.001$; ****: $p \leq 0.0001$).

	Phenolics % of plant species				**Alkaloids** % of plant species			
Site	**0**	**±/+**	**++/+++**		**0**	**±/+**	**++/+++**	
Mid-montane rain forest (Andasibe)	10.8	13.2	76.0	(n=129)	36.7	25.0	38.3	(n=128)
Gallery forest (Berenty)	27.0	27.8	45.2	(n=115)****	15.4	27.9	56.7	(n=104)***
Spiny bush (Berenty)	28.6	35.7	35.7	(n=42)****	11.8	27.5	60.8	(n=51)**

The distribution of phenolics in plants at Andasibe differs significantly from that found in the two forest types at Berenty. Plants responding ++ and +++ account for much of the difference. Conversely, the plants at Andasibe are more frequently poor in alkaloids compared with the other two forests. It is noticeable however that, in all three sites, proportions of plants that give strong positive responses to alkaloid reagents are higher than those found in many other primate habitats, including lemur habitats (e.g. dry deciduous forest of Morondava; A. Hladik, 1980). It must be stressed that the reagents used to detect these substances are not totally specific (preliminary results are presented here). In addition, the high alkaloid content found in both the rainforest (Andasibe) and gallery forest (Berenty) can be explained by the large number, in our samples, of species living in open habitats (pioneer species, or introduced plants). The open parts of a rainforest, with a relatively low plant diversity, present a high frequency of alkaloid-rich plants (Hladik and Hladik, 1977), as in the case of white-sand riverine forests (see above).

Table 2. Comparison of dietary plants selected by three lemur species, with a random sample of the gallery forest (at Berenty), according to the screening of phenolics and alkaloids. The significance of the differences derives from Chi-square tests (*: $p \leq 0.05$). The difference between the distribution of alkaloids in *L. catta*'s diet and alkaloids in the gallery forest is close ($p=0.07$) to the level of significance. a: In *E. fulvus*, which exhibits a low dietary diversity, results were grouped in two classes to apply the statistical test with the continuity correction.

	Phenolics % of plant samples				**Alkaloids** % of plant samples			
Lemur species	**0**	**±/+**	**++/+++**		**0**	**±/+**	**++/+++**	
Propithecus verreauxi	14.7	38.2	47.1	(n=34)	15.6	31.2	53.1	(n=32)
Lemur catta	55.6	27.8	16.7	(n=18)*	27.8	44.4	27.8	(n=18)
Eulemur fulvus[a]	75.0		25.0	(n=8)	62.5		37.5	(n=8)
Gallery forest (Berenty)	27.0	27.8	45.2	(n=115)	15.4	27.9	56.7	(n=104)

In May/June 1998, the diet of sympatric groups of three species, *Lemur catta*, *Eulemur fulvus* (introduced population), and *Propithecus verreauxi* was studied in terms of the relative proportions of ingested matter, in the gallery forest of Berenty. A total of 46 leaf species was observed to be eaten by *Propithecus*, versus 22 by *Lemur catta*, and 9 by *Eulemur fulvus*.

Table 2 shows the alkaloid and phenolic contents (according to screening tests) of a subset of the leaves selected by each of the three species, as compared with a random sample of plants available in the habitat. Plants tested accounted for more than 70% of the diets (by weight). It may be seen that only *Lemur catta* choose plants with low phenolics and tends to avoid plants containing alkaloids (the difference, however, is not significant, with p=0.07). The distribution of these secondary compounds in the diet of the other two species do not differ significantly from that of the random sample. For instance, *Propithecus verreauxi* can feed on the tannin-rich leaves of *Vernonia pectoralis* (Asteraceae) in the gallery forest of Berenty (Fig. 4).

Figure 4. *Propithecus verreauxi* feeding on the tannin-rich leaves of *Vernonia pectoralis* (Asteraceae) in the gallery forest of Berenty (photo B. Simmen, June 1998)

Phenolic compounds include tannins as well as non-tannins molecules, and, as discussed above, the occurrence of alkaloids and tannins does not necessarily imply toxic or digestibility-reducing effects. For instance, one of the most common fruit at Berenty, in December, *Rinorea greveana*, that responded positively to the alkaloid reagents, was eaten by all lemur species including *Lemur catta* (Fig. 5). However, the fact that *L. catta* tends to avoid many plants that respond positively suggests that leaves actually have a deterrent effect, probably mediated by alkaloids and/or tannins. We also observed a few cases of geophagy in *L. catta*, a behavior that, besides other beneficent effects, may efficiently reduce tannin activity through adsorption by earth (Johns & Duquette, 1991; Setz et al.., in press).

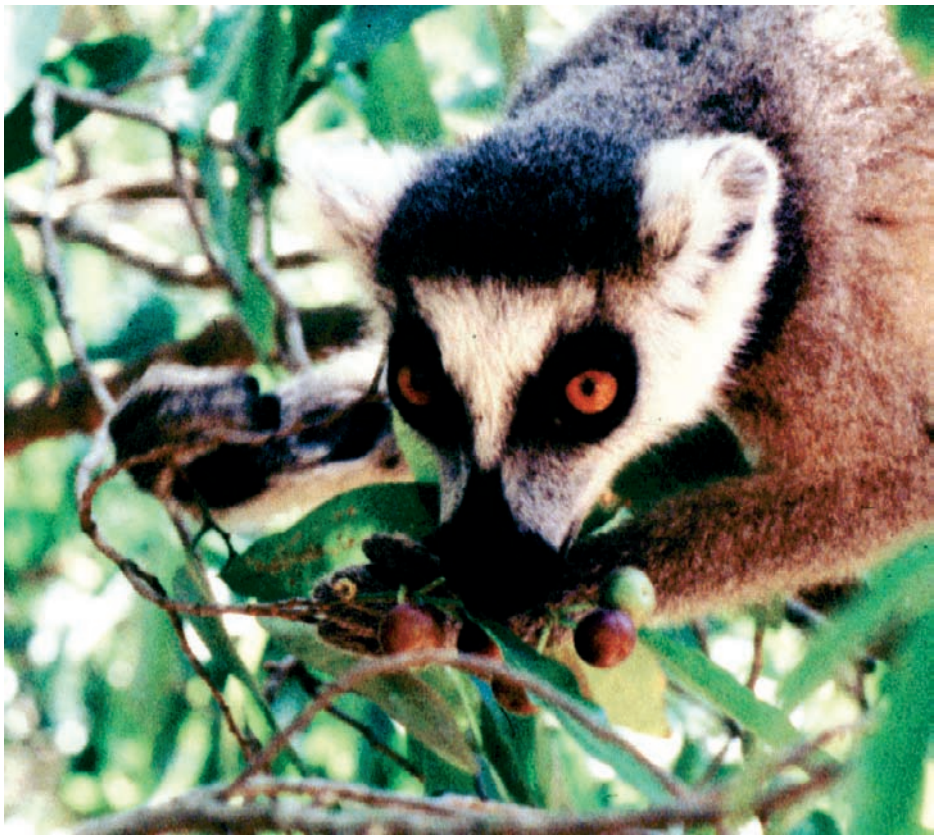

Figure 5. *Lemur catta* feeding on fruits of *Rinorea greveana* in the gallery forest of Berenty (photo C.M. Hladik, December 1997)

When testing solutions of pure tannic acid with the tannin reagents, large precipitates were obtained for concentrations higher than 0.4g/l. Accordingly, this might correspond to the tolerance threshold of *Lemur catta*. In the case of *Propithecus verreauxi*, much larger amounts are required (above 170g/l) to depress the ingestion of mixtures of sucrose with tannic acid (Dennys, 1991). In the eastern rain forest of Andasibe, the tolerance of condensed tannins and alkaloids in *Eulemur fulvus* (Ganzhorn, 1988), a phenomenon that is apparently similar in Berenty, might also be related to a low taste sensitivity.

Such data provide evidence that different abilities to taste bitter or astringent compounds may explain food choices of different species living in the same habitat. It is likely that lemur species having evolved distinct sensibilities also have to adjust food choices in relation to the relative abundance of plant secondary compounds in different habitats.

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Appendix

List of the specimens tested for phenolics and alkaloids, in the mid-montane forest (at Andasibe) and, (at Berenty) in the thorny bush (B) and the gallery forest (F), eventually planted (Pl). The herbarium specimens have been collected by A. Hladik (Ref. AH), and by B. Simmen and P. Ramasiarisoa (Ref. M), with tentative identification for sterile specimens.

Andasibe

FAMILY	*Species*	Ref.	Phenolics		Alkaloids	
			Salt. gel.	$FeCl_3$	Mayer	Drag.
ACANTHACEAE	***Strobilanthes* sp.**	M 74	0	0	0	+
" (?)	(unidentified)	AH 6229	0	++	0	0
ANACARDIACEAE	***Protorhus cf. ditimena*** Perr.	M 29	±	++	0	0
"	***Protorhus thouvenotii*** Lecomte	M 25	++	++	0	+
ANNONACEAE	***Artabotrys* sp.**	M 60	++	++	++	++
"	***Xylopia* sp.**	M 35	+++	+	++	++
"	(unidentified)	M 65	+	++	++	±
APOCYNACEAE	***Carissa edulis*** Vahl	M 26	++	+	0	±
"	(unidentified)	AH 6213	0	+	0	0
AQUIFOLIACEAE	***Ilex mitis*** (L.) Radlk.	M 1	+	++	++	++
ARALIACEAE	***Polyscias* sp.**	M 41	+++	+++	0	0
"	***Schefflera* sp.**	AH 6167	++	0	0	0
"	***cf. Cussonia***	AH 6179	±	±	0	0
ASTERACEAE	***Ageratum conyzioides*** L.	AH 6190	±	++	+	+
"	***Emilia humifusa*** D.C.	AH 6029	±	+++	+	+
"	***Emilia* sp.**	AH 6192	0	++	0	0
"	***Psiadia altissima*** Benth. & Hook.	AH 6027	+	+++	±	++
"	***Vernonia* sp.**	AH 6161	+	+++	0	0
BURSERACEAE (?)	(unidentified)	AH 6209	+	++	0	0
CHLAENACEAE	***Rhodolaena bakeriana*** Baill.	M 31	+++	+++	±	++
CONVOLVULACEAE	***Merremia tridentata*** (L.) Hallier	AH 6195	+++	+++	0	0
CUNNIONACEAE	***Weinmannia bojeriana*** Tul.	M 52	+++	+++	0	0
"	***Weimmania rutembergii*** Engl.	M 16	++	++	0	0
CYPERACEAE	***Carex* sp.**	AH 6228	0	0	0	0
DIOSCOREACEAE	***Dioscorea* sp.**	AH 6039	++	++	±	±
EBENACEAE	***Diospyros* sp.**	M 54	+++	+++	0	+
"	***Diospyros* sp.**	M 63	+++	+++	±	++
ERICACEAE	***Philippia* sp.**	AH 6263	+++	++	0	0
ERYTHROXYLACEAE	***Erythroxylum nitidulum*** Bak.	AH 6217	+++	+++	++	++
EUPHORBIACEAE	***Suregada cf. laurina*** Baill.	M 33	0	+	±	+
"	***Blotia* sp.**	M 19	0	0	0	0
"	***Bridelia tulasneana*** Baill.	AH 6186	+	+++	0	++
"	***Croton mongue*** Baill.	AH 6211	+	+	0	0
"	***Lautembergia* sp.**	M 59bis	0	0	+++	++
"	***Macaranga alnifolia*** Bak.	M 5	+++	+++		
"	***Macaranga alnifolia*** Bak.	AH 6005			±	++
"	***Macaranga obovata*** Bak.	AH 6004	++	+++	0	++
"	***Macaranga cf. ankafinensis*** Baill.	AH 6180	++	++	±	+
"	***Macaranga* sp.**	AH 6202	++	+++	0	0
"	***Uapaca densifolia*** Bak.	AH 6182	++	++	0	0
"	***Uapaca* sp.**	AH 6183	+	++	0	0
FLACOURTIACEAE	***Aphloia theiformis*** Benn.	M 3	±	+++	0	±
GUTTIFERAE	***Garcinia chapeleri*** (Planch. & T.) Perr.	M 28	++	++	0	++
"	***Mammea* sp.**	M 36	++	++	0	+
"	***Symphonia louvelii*** Jum. & Perr.	M 27	+++	+++	±	±
"	***Symphonia tanalensis*** Jum. et Perr.	M 11	++	++	0	0
HYPERICACEAE	***Harungana madagascariensis*** Choisy	M 7	++	+	0	++
"	***Psorospermum androsaemifolium*** Bak.	M 57	++	±	++	+++
LAURACEAE	***Ocotea similis*** Kosterm.	M 18	0	+	+	±
"	***Ocotea* sp.**	AH 5820			+	+
"	***Ocotea* sp.**	AH 6212	+++	+++	+++	±
"	***Ravensara crassifolia*** (Bak.) Danguy	M 37			+	+
"	***Ravensara ovalifolia*** Danguy	M 46	++	+		
"	***Ravensara* sp.**	AH 6003	0	0	0	0

LILIACEAE	***Dianella ensifolia*** (L.) Redouté	M 45	±	±	0	0
"	***Dianella* sp.**	M 67	++	++	0	0
LOGANIACEAE	***Anthocleista madagascariensis*** Bak.	M 10	0	0		
"	***Anthocleista rhizophoroides*** Bak.	M 55	0	0	0	±
"	***Anthocleista* sp.**	AH 6045	±	±	++	++
"	***Buddleia* sp.**	AH 6246	+	+	+++	++
MALVACEAE	***Sida rhombifolia*** L.	AH 6036	0	+	0	0
"	***Urena lobata*** L.	AH 6037	++	+++	0	0
MELASTOMATACEAE	***Clidemia hirta*** G. Don	M 8	+++	+++	+	+++
"	***Dichaetanthera oblongifolia*** Bak.	AH 6016	+	++	0	0
"	***Dichaetanthera* sp.**	M 73	+	+++	0	+
"	***Medinilla cf. occidentalis*** Naud.	M 49	++	+++	0	±
"	***Medinilla* sp.**	M 22			0	0
"	***Medinilla* sp.**	M 34	++	+	0	±
"	***Tristemma mauritianum*** Gmel.	M 72	++	+++	±	++
MIMOSACEAE	***Acacia delbeata*** Link.	AH 6063	+++	+++	+++	+++
"	***Albizia gummifera*** (Gmel.) G.A. Smith	AH 6002	0	0	++	++
"	***Albizia chinensis*** (Osb.) Merr.	AH 6042	0	++	++	++
"	***Dichrostachys cf. tenuifolia*** Benth.	AH 6006	±	+	++	+
MONIMIACEAE	***Tambourissa trichophylla*** Bak.	M 38	++	0		
"	***Tambourissa purpurea*** (Tul.) A. DC.	AH 6196	+++	+++	+	±
MORACEAE	***Bosqueia* sp.**	AH 6197	+++	+++	++	++
"	***Ficus* sp.**	AH 6039bis	++	+++	0	0
"	***Ficus* sp.**	AH 6201	±	±	±	±
"	***Pachytrophe dimepate*** Bur.	M17	+++	+++	0	0
"	(unidentified)	AH 6214	+	+++	0	0
MYRICACEAE	***Myrica spathulata*** Mirbel	AH 6218	+	++	0	0
MYRSINACEAE	***Oncostemum* sp.**	M 15	++	+		
"	***Oncostemum* sp.**	M 32			++	++
"	***Oncostemum* sp.**	M 42	++	++	0	0
"	***Oncostemum* sp.**	M 47	++	++	+	++
MYRTACEAE	***Eucalyptus* sp.**	AH 6021	++	+++	+++	+++
"	***Eugenia goviala*** H. Perr.	M 20	++	+++	±	++
"	***Eugenia* sp.**	M 58	++	+++		
"	***Eugenia* sp.**	AH 6200	++	+++	0	0
"	***Psidium cattleyanum*** Sabine	M 71	+	+++	±	++
"	***Psidium guayava*** Berg	M 70	++	+++	0	++
OCHNACEAE	***Campylospermum lanceolatum*** (Bak.)Perr.	M 39	0	0	0	0
"	***Campylospermum anceps*** (Bak.)Perr.	M 13	++	++	+	+
OENOTHERACEAE	***Jussiaea* sp.**	AH 6024	++	+++	0	0
OLEACEAE	***Noronhia* sp.**	M 12	++	++	0	++
PANDANACEAE	***Pandanus* sp.**	AH 6166	0	++	±	+
PAPILIONACEAE	***Dalbergia monticola*** Bosser & Rabe.	M 48	++	+++	+	++
PASSIFLORAE	***Passiflora foetida*** L.	AH 6035	0	+++	++	++
"	***Passiflora incarnata*** L.	AH 6026	0	+	+++	+++
RHIZOPHORACEAE	***Cassipourea* sp.**	AH 6199	0	++	0	0
ROSACEAE	***Rubus roridus*** Lindl.	AH 6019	+++	+++	+	++
"	***Rubus rosaefolius*** Smith	AH 6007	++	+++	+	+++
RUBIACEAE	***Canthium* sp.**	M 33bis	++	++	++	++
"	***Coffea* sp.**	AH 6243	++	+++	++	+
"	***Danais* sp.**	AH 6203	±	±	0	0
"	***Enterospermum* sp.**	M 9	0	0	++	+
"	***Gaertnera macrostipula*** Lam.	M 4	++	++	0	+
"	***Rothmannia* sp.**	M 24	0	±	+	+
"	***Sabicea diversifolia*** Pers.	AH 6040	+++	+++	+	++
"	(unidentified)	AH 6216	+	++	0	0
"	***Pyrostria* sp.**	AH 6230	0	0	++	+
" (?)	(unidentified)	AH 6215	+	+++	0	0
SAPINDACEAE	***Allophyllus cobbe*** (L.) Raeusch.	M 53	+	0	0	0
"	***Filicium decipiens*** (W.&A.) Thw.	AH 6163	++	++	0	±
SAPOTACEAE	***Gambeya boiviniana*** (Pierre) Aubrév.	M 171	++	++	+	+
SMILACACEAE	***Smilax kraussiana*** Meissn.	AH 6032	+	++	0	0
SOLANACEAE	***Solanum auriculatum*** Ait	M 68	0	0	++	++
"	***Solanum* sp.**	M 64	+	+++	+	+
STERCULIACEAE	***Dombeya* sp.**	AH 6012	++	++	0	0
"	***Dombeya* sp.**	AH 6014	0	0	±	+

STRELIZIACEAE	***Ravenala madagascariensis*** Gmel.	AH 6018	++	0	+	+
THEACEAE	***Camellia thaeiformis*** Hance	AH 6015	+++	+++	+	++
ULMACEAE	***Trema orientalis*** Bl.	M 69	++	+++	++	++
VACCINACEAE	***Vaccinium* sp.**	M 21	+++	+++	0	++
VERBENACEAE	***Clerodendron* sp.**	AH 6177	+	+	++	0
"	***Lantana camara*** L.	AH 6040bis	++	+++	0	0
"	***Stachytarpheta jamaicensis*** Vahl	AH 6043	0	0	0	0
ZINGIBERACEAE	***Aframomum angustifolium*** K. Schum.	AH 6033	++	0	0	++
"	***Hedychium coronarium*** Kœniz	AH 6033bis	++	+	0	+
(unidentified family)		M 51	++	++	++	++
Pteridophytes:						
DENNSTAEDTIACEAE	***Pteridium aquilinum*** (L.) Kühn.	AH 6030	++	+++	0	±
GLEICHENIACEAE	***Dicranopteris linearis*** (Burm.) Under.	AH 6176	+++	+++	0	0
"	***Sticherus flagellaris*** (Bory) St John	AH 6164	±	+	0	0
SCHIZAEACEAE	***Lygodium lanceolatum*** Desv.	AH 6189	0	++	0	0

Berenty

FAMILY	*Species*	Ref.	B/F	Phenolics		Alkaloids	
				Salt. gel.	$FeCl_3$	Mayer	Drag.
ACANTHACEAE	***Crossandra poissonii*** R. Ben.	M175	F	0	++	0	+
"	***Hypoestes* sp.**	M261	F	±	++	0	+
" (?)	(unidentified)	M131	B	0	++	+	++
AGAVACEAE	***Sanseveria* sp.**	M269	F/Pl	0	0	0	+
AMARANTHACEAE	***Aerva madagassica*** Suess.	M308	B	±	0	++	+
ANACARDIACEAE	***Operculicarya cf. decaryi*** H. Perr.	M338	F/Pl	++	+	0	++
"	***Poupartia caffra*** (Sond.) H. Perr.	M306	B/Pl	+++	+++	+++	+++
"	***Poupartia minor*** (Boj.) Marchand	M208	F/Pl	++	0	0	++
ANNONACEAE	***Annona* sp.**	M244	F/Pl	0	0	++	++
APOCYNACEAE	***Hazunta modesta*** (Bak.) Pichon	M255	F	0	+++	+++	+++
"	***Catharanthus roseus*** (L.) G. Don	M333	F	0	±	++	++
"	***Plectaneia* sp.**	M316	B	0	0	++	+++
ARISTOLOCHIACEAE	***Aristolochia* sp.**	M235	F	0	0		
"	***Aristolochia* sp.**	M229	F			+++	+++
ASCLEPIADACEAE	***Leptadenia madagascariensis*** Decne.	M134	B	±	+	++	++
"	***Leptadenia* sp.**	M225	F	0	0	+	0
"	***Leptadenia* sp.**	M285	F	±	+++	++	++
"	***Pervillea decaryi*** (Choux) Klack.	M144	B	±	±	++	+++
"	***Ceropegia* sp.**	M336	F	0	+		
"	***Cynanchum* sp.**	AH 5905	B			+	±
"	***cf. Marsdenia* sp.**	M319	B	0	0	0	+
"	***cf. Secamone* sp.**	M288	F	±	+++		
"	(unidentified)	M195	F			+++	++
"	(unidentified)	M195bis	F	0	++		
"	(unidentified)	M238	F	0	0	0	±
ASTERACEAE	***Vernonia pectoralis*** Bak.	M205	F	+	+++	0	0
"	***cf. Vernonia* sp.**	M286	F	±	+++		
"	(unidentified)	M188	F	+	+++	+	++
"	(unidentified)	M280	F	±	±	±	±
BIGNONIACEAE	***Fernandoa madagascariensis*** (Bak.) Gent.	M332	F/Pl	++	++	+	+
BORAGINACEAE	***Cordia rothii*** Roem. & Schult.	M107	F/Pl	±	+++	0	0
"	***Cordia* sp.**	M304	F	±	0		
"	***Cordia* sp.**	M165	F			++	++
BURSERACEAE	***Commiphora* sp.**	M122	B	+	++	±	+++
"	***Commiphora* sp.**	M130	B	+	+	0	+
"	***cf. Commiphora* sp.**	M196	F	+	++	0	0
CACTACEAE	***Opuntia vulgaris*** Miller		F/Pl	0	0	+	+

CAESALPINIACEAE	***Tetrapterocarpon geayi*** H. Humb.	M125	B	0	±	++	+++
"	***Bauhinia grandidieri*** Baill.	M132	B	+	+	++	+++
"	***Bauhinia* sp.**	M158	F	+	++		
"	***Caesalpinia bonduc*** Roxb.	M259	F	0	0	++	++
"	***Cassia siamea*** Lam.	M236	F/Pl	0	+++	±	+++
"	***Cassia* sp.**	M232	F/Pl	0	0	++	+++
"	***Delonix regia*** (Hook.) Raf.	AH 5986	F/Pl	++	+++	+	++
"	***Tamarindus indica*** L.	M234	F	++	+	0	+
CAPPARIDACEAE	***Boscia longifolia*** Hadj Moust.	M133	B			0	+
"	***Boscia longifolia*** Hadj Moust.	M143	B	0	0	+	+++
"	***Cadaba virgata*** Boj.	M267	F	±	±		
"	***Cadaba virgata*** Boj.	AH 5976	F			++	+++
"	***Capparis sepiara*** L.	M102	F	0	0		
"	***Capparis* sp.**	M270	F			+	+
"	***Crataeva greveana*** Baill.	M262	F	0	++		
"	***Crataeva* sp.**	M105	F			++	++
"	***Crataeva* sp.**	M263	F	0	0		
"	***Maerua filiformis*** Drake	M295	F/B	0	+++		
"	***Maerua filiformis*** Drake	AH 5968	F /B			0	++
CELASTRACEAE	***Evonymiopsis longipes*** Perr.	M317	B	±	0	+	+
COMBRETACEAE	***Combretum* sp.**	M192	F	+++	+++	++	++
"	***cf. Terminalia* sp.**	M313	B	++	+++	0	0
COMMELINACEAE	***Commelina* sp.**	M257	F	±	++	+	+
CONVOLVULACEAE	***Hildebrandtia promontorii*** Deroin	AH 5969	B			±	+
"	***Hildebrandtia valo*** Deroin	M310	B	0	++	+	+
"	***Ipomoea cairica*** (L.) Sweet	M201	F	0	±	0	0
CRASSULACEAE	***Kalanchoe beauverdii*** Hamet	M283	F	++	++	0	0
"	***Kalanchoe beharensis*** Drake		F/Pl	0	0	0	0
CUCURBITACEAE	***Xerosicyos decaryi*** Guill.	M282	F	+	+	+++	+++
"	***cf. Zehneria* sp.**	M264	F	0	±	+	++
DIDIEREACEAE	***Alluaudia ascendens*** Drake	M149	B	0	0	0	0
"	***Alluaudia procera*** Drake	M146	B	0	0	0	0
DIOSCOREACEAE	***Dioscorea fandra*** Perr.	AH 5980	B			0	0
"	***Dioscorea nako*** Perr.	M345	F	0	0		
"	***Dioscorea nako*** Perr.	AH 5978	B			±	++
EUPHORBIACEAE	***Acalypha* sp.**	M109bis	F	++	+++	+++	+++
"	***Acalypha* sp.**	M109	F	+	+++	++	+++
"	***Croton* sp.**	M178	F	++	+	++	++
"	***Euphorbia* sp.**	M142	B	0	0	0	+
"	***Euphorbia* sp.**	M213	F/Pl	±	0	+	+
"	***Phyllanthus casticum*** Willem.	M186	F	+++	+++		
"	***Phyllanthus casticum*** Willem.	M110	F			++	+++
"	***Securinega cf. capuronii*** Léandri	AH 5971	B			++	+++
"	***Croton* sp.**	M138	B			0	+
"	***Croton* sp.**	M324	B			++	+
"	***cf. Sclerocroton melanostictus***	M116	B			±	++
FLACOURTIACEAE	***Flacourtia indica*** (Burm.) Merril.	M217	F/Pl	++	+++	±	±
"	***Physena sessiliflora*** Tul.	M206	F	+	+	+	+
HIPPOCRATEACEAE	***cf. Hippocratea* sp.**	AH 5903	B	++	±	++	++
"	***cf. Loesneriellia* sp.**	M243	F	+++	+++	+++	+++
"	***cf. Loesneriellia* sp.**	M273	F	±	+	++	++
"	(unidentified)	AH 5907	F			++	++
LILIACEAE	***Aloe vahombe*** Decorse		F/Pl	0	0	0	0
"	***Aloe cf. capitata*** Bak.		F/Pl	0	0	±	±
LOGANIACEAE	***Strychnos* sp.**	M252	F	±	+	+++	+++
"	***Strychnos* sp.**	M294	B	0	0	+++	+++
MALPIGHIACEAE	***Tristellateia* sp.**	M337	F	0	0		
MALVACEAE	***Abutilon pseudocleistoganum*** Hochr.	M239	F	0	0	0	±
"	***Hibiscus* sp.**	M180	F	+++	+++	±	+
"	***Hibiscus* sp.**	M318	B	±	+	0	++
"	***Hibiscus* sp.**	M117	B	0	+++	++	+
"	***Hibiscus* sp.**	M127	B	+	++	++	++
"	***Megistostegium nodulosum*** (Drake) Hochr.	AH 5988	B	+	++	0	0
MELIACEAE	***Azadirachta indica*** Jussieu	M166	F/Pl	0	0	++	++
"	***Melia azedarach*** L.	M330	F/Pl	0	0	++	+++
"	***Quivisianthe papinae*** Baill.	M223	B/F	+	0		
"	***Quivisianthe papinae*** Baill.	M137	B/F			++	++
"	***cf. Cedrelopsis grevei***	M124	B	0	±		
"	***cf. Turraea* sp.**	M245	F	0	0	±	+

MENISPERMACEAE	(unidentified)	M341	F	+	++		
MIMOSACEAE	***Acacia rovumae*** Oliv.	M214	F	+	±	++	++
"	***Acacia* sp.**	M342	F	0	0		
"	***Albizzia polyphylla*** Fourn.	M293	F	++	++	++	++
"	***Dicrostachys* sp.**	M118	B	+	++	0	+
"	***Leucaena glauca*** (L.) Benth.	M211	F/Pl	±	+	++	+
"	***Pithecellobium dulce*** Benth.	M170	F/Pl	++	+		
"	***Pithecellobium dulce*** Benth.	M212	F/Pl			+++	+++
"	(unidentified)	M275	F	++	0	+	+
MORACEAE	***Ficus cf. trichopoda*** Bak.	M329	F	0	0	0	0
"	***Ficus cf. cocculifolia*** Bak.	M305	F	+++	+++		
"	***Ficus cf. megapoda*** Bak.	M179	F	0	0	0	++
"	***Ficus cf. grevei*** Baill.	M299	F			0	+
"	***Ficus cf. grevei*** Baill.	M300	F	+	+++		
"	***Ficus* sp.**	M301	F	+++	±	±	+
"	***Ficus* sp.**	M198	F	0	+	0	+
MYRTACEAE	***Eucalyptus* sp.**	M216	F/Pl	++	+++	++	++
NYCTAGINACEAE	***Bougainvillaea spectabilis*** Willd.	M231	F/Pl	+	+	+	+
"	***Commicarpus commersonii*** Cav.	M265	F	0	+	++	++
PAPILIONACEAE	***Clitoria heterophylla*** Lam.	M128	B			++	++
"	***Mundulea scoparia*** R. Viguier	M115	B	0	±	++	++
"	(unidentified)	M284	F	0	+++	++	++
POACEAE	***Phragmites mauritianus*** Kunth.	M276	F	0	++	++	+++
RHAMNACEAE	***Colubrina* sp.**	M291	F	±	±	+	±
"	***Zizyphus* sp.**	M254	F	0	+++	++	++
RUBIACEAE	***Enterospermum* sp.**	M221	F	0	±		
"	***Enterospermum* sp.**	M181	F			+++	+++
"	***Enterospermum* sp.**	M260	F	0	++		
"	(unidentified)	M260bis	F	±	±		
"	(unidentified)	M292	F	+	+++	+++	+++
RUTACEAE (?)	(unidentified)	M164	F	+	±	0	++
"	(unidentified)	M302	F	0	0	+	+
SALVADORACEAE	***Azima tetracantha*** Lam.	M162	F	0	0	+	++
"	***Salvadora angustifolia*** Turrill.	M272	F/B	0	0	+	++
SAPINDACEAE	***Neotina isoneura*** (Radlk.) Capuron	M187	F	+	0	0	0
SOLANACEAE	***Solanum batoides*** d'Arcy & Rak.	M120	B	0	0		
"	***Solanum croatii*** d'Arcy & Keat.	AH 5972	F/B	+	++	+++	++
STERCULIACEAE	***cf. Byttneria* sp.**	M161	F	+	+	+	++
TILIACEAE	***Grewia grevei*** Baill.	M126	B	++	+++	±	++
"	***Grewia* sp.**	M321	F/B	0	0	0	±
"	***Grewia* sp.**	M242	F	±	0	++	++
"	***Grewia* sp.**	M343	F	0	++		
ULMACEAE	***Celtis bifida*** Leroy	M230	F	+	+	0	0
"	***Celtis philippensis*** Blanco	M114	F	+	+	++	++
"	***Trema orientalis*** Blume	M340	F	0	0		
VERBENACEAE	***Clerodendron* sp.**	M322	B	+	±		
" (?)	***cf. Clerodendron* sp.**	M312	B			++	++
VIOLACEAE	***Rinorea greveana*** H. Bn	M154	F	+	++	++	+++
VITACEAE	***Cissus quadrangularis*** L.		F	±	±	+	+
(unidentified family)		M251	F	0	+	++	+
(unidentified family)		M246	F	0	+	++	+
(unidentified family)		M290	F	+	+	0	++
(unidentified family)		M227	F	0	0	0	0
(unidentified family)		M326	F	0	0		
(unidentified family)		M193	F			0	0
(unidentified family)		M147	B	0	0	+++	+++
(unidentified family)		M328	F	0	±	++	++
(unidentified family)		AH 5901	B			++	±
(unidentified family)		M129	B	+	+++		
(unidentified family)		M135	B	+	+		
(unidentified family)		M287	F	++	++	++	±
(unidentified family)		M121	B/F	+	++	0	0
(unidentified family)		M258	F	±	+++		
(unidentified family)		M256	F	+	+++	±	±
(unidentified family)		M250	F	0	0	+++	+++
(unidentified family)		M279	F			0	0
(unidentified family)		M281	F			0	0
(unidentified family)		M311	B	0	0	±	+
(unidentified family)		M331	F	+++	+++	0	++
(unidentified family)		M320	B	0	+	+++	+++